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An *Alu* Insertion Polymorphism in a Baboon Hybrid Zone

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ABSTRACT A novel polymerase chain reaction (PCR) primer pair was used to analyze the frequency of insertion of the first described, nonhuman, baboon-specific *Alu* repetitive element in populations from the *Papio hamadryas anubis* and the *Papio hamadryas hamadryas* subspecies, and from a number of *anubis-hamadryas* hybrids. The *Alu* insertion is found in intron 7 of the baboon lipoprotein lipase (LPL) gene. Each of the populations had different frequencies for the insertion, and the hybrids examined had a frequency intermediate to that of the parental populations. All hybrids and all *P. h. anubis* groups except the group of *anubis* sampled in 1973 exhibited higher-than-expected heterozygosity, while *P. h. hamadryas* and 1973 *P. h. anubis* showed lower-than-expected heterozygosity, supporting behavioral and other genetic observations of greater *anubis* outbreeding relative to *hamadryas*. This may include asymmetric introgression of the *Alu* insertion from *hamadryas* to the *anubis* population due to hybridization. Am J Phys Anthropol 109:1–8, 1999.

The *Alu* family of elements consists of over 500,000 copies of a retroposed element dispersed throughout the human haploid genome (Novick et al., 1994). *Alus* are named after the restriction enzyme *Alu* I, which cleaves most *Alu* elements (Houck et al., 1979). *Alu* elements comprise the most numerous family of short interspersed repetitive elements (SINEs) in the human genome (von Sternberg et al., 1992), and they have been detected in all primates examined (Novick et al., 1996). *Alu* elements are thought to be derived from the signal recognition particle 7SL RNA gene, based on the 90% sequence similarity they share (Ullu and Tschudi, 1984). However, the 7SL gene has a 150 bp segment that is absent in *Alu* sequences (Deininger, 1989). Most *Alus* are around 300 nucleotides (nt) in length. Their structure is organized in a dimeric fashion, the right monomer being 31 nts longer than the left, while the left monomer includes boxes A and B of the RNA polymerase III split internal promoter (Fuhrman et al., 1981). Also characteristic of *Alu* elements is an adenosine-rich area between the two dimers and a poly A tract at the 3'-end of the repetitive element which is representative of most SINEs (Economou et al., 1990).

Alus have been used to infer human phylogenies (Novick et al., 1993, 1995, 1996, 1998; Batzer et al., 1994; Thomas and Herrera, 1998). They are particularly useful in phylogenetic studies because they are pre-

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sumably neutral and, unlike most other polymorphisms, the ancestral state (the lack of insertion) is known. Furthermore, an *Alu* insertion event can be assumed to have occurred only once in any particular genomic location, since the probability of two independent insertions in the same position is remote (Novick et al., 1994; Szmulewicz et al., 1998). Partial deletion events have been reported but invariably leave genetic residues behind (Ariga et al., 1990). For these reasons, *Alu* insertions have often been treated as "Dollo" characters in phylogenetic analyses, i.e., a character that can be gained only once, but lost many times (Farris, 1977).

Alus can be subdivided into different subfamilies according to diagnostic sites within the *Alu*, and it is known that the different subfamilies underwent extensive retroposition at different periods of primate evolution (Kapitanov and Jurka, 1996). There are several published nomenclatures for *Alu* subfamilies, the most widely used being that of Batzer et al. (1996). To date, only one nonhuman polymorphic *Alu* repeat has been found, and it is located in intron 7 of the lipoprotein lipase (LPL) gene. According to Cole et al. (1997), this *Alu* belongs to the Y subfamily which corresponds to the *Alu* IV subfamily of Batzer et al. (1996).

The presence and absence of a particular *Alu* in specific evolutionary lineages can be used to infer its date of insertion. Based on their distribution pattern in primate lineages, the *Alu* IV subfamily most probably originated approximately 60 million years ago (Ma). The average *Alu* IV was inserted about 30 Ma, and these are still actively retrotransposing (Britten et al., 1988).

We used the LPL polymorphic *Alu* insertion to generate allelic frequencies for two ecologically, phenotypically, and socially well-differentiated baboon subspecies: *Papio hamadryas hamadryas* (found in northeast African semiarid deserts, including the Ethiopian lowlands), *P. h. anubis* (occurring in the wetter highlands and savannas), and a number of *hamadryas* × *anubis* hybrids and their backcrosses, found at their boundary in Ethiopia's Awash National Park. Hybridization is the interbreeding of individuals from two populations, or groups of populations, which are distinguishable on the basis of one or more heritable characters (Harrison, 1993). First reported in 1968 (Kummer, 1990; Nagel, 1973; Phillips-Conroy and Jolly, 1986), the Awash National Park hybrid zone contains many phenotypic hybrids and backcross individuals. *Anubis*, or olive baboons, occur in forest and savanna habitats from Sierra Leone to Tanzania. Both sexes have olive-brown fur, and dark facial and paracallosal skin. *Hamadryas* baboons are slightly smaller than *anubis*. Males have bright red facial skin and buttock-pads, and a striking mane of long, multiringed gray hairs. Females (and young) are maneless, with plain brown fur and dusky-pink facial skin (Jolly, 1993).

These populations have been the subject of extensive behavioral observation and systematic trap-and-release sampling since 1973 (Phillips-Conroy and Jolly, 1986; Phillips-Conroy et al., 1991). In recent years, an abundance of evidence from genetic markers has increased our understanding of the direction and dynamics of hybridization in the Awash National Park, Africa (Jolly and Brett, 1973; Brett et al., 1982; Newman and Disotell, 1997; Woolley-Barker, 1998). Evidence from the *Alu* marker adds to this understanding. Our results indicate that the two baboon subspecies exhibit different frequencies for this polymorphic *Alu* insertion. The hybrid population from the area of overlap possesses a frequency intermediate to that of the two subspecies. These results from the LPL locus provide further genetic evidence of introgression between the parental subspecies in the hybrid zone.

MATERIALS AND METHODS

Populations studied

We analyzed three classes of baboons from two different subspecies. *Papio hamadryas hamadryas*, *Papio h. anubis*, and *hamadryas-anubis* hybrids were captured in the Awash National Park in Ethiopia, using a standard protocol developed and used since 1973 (Brett et al., 1982) on three different collection dates from different groups, spanning 24 years. Figure 1 provides a map indicating the collection sites within the Awash National Park. In total, 179 individuals were examined. The sample size and collection dates for each class are as follows:

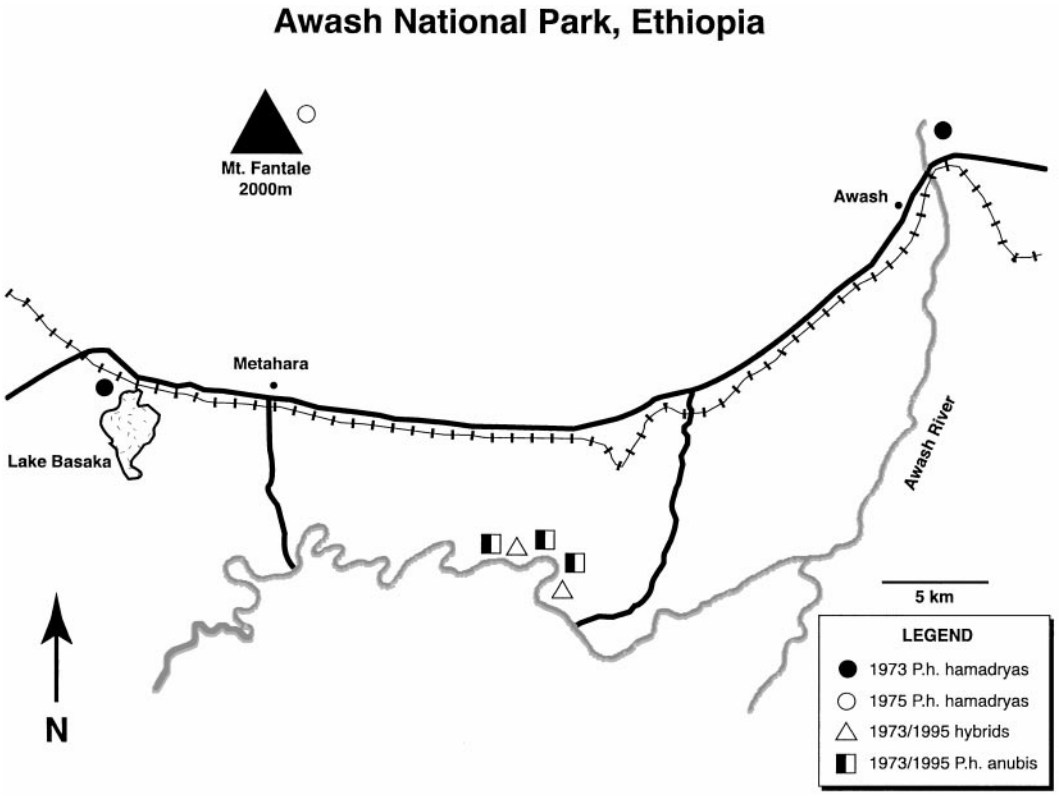

Fig. 1. Collection sites in Awash National Park, Ethiopia.

39 in 1973, 27 in 1997 (*P. h. hamadryas*); 42 in 1973, 16 in 1995 (*P. h. anubis*); 37 in 1973, 18 in 1995 (*hamadryas* × *anubis* hybrids). Organisms classified as hybrids include F1 hybrids, backcrosses, and intercrosses. No effort was made to distinguish among these types of hybrids. The organisms were identified and classified using the hybrid index of Nagel (1973).

DNA extraction and PCR amplification

Blood was drawn from the femoral vein into heparinized Vacutainer (Becton Dickinson) tubes, and then centrifuged in the field for 25 min at 3,000 rpm. Buffy coats and red blood cells were stored in liquid nitrogen (LN2) until reaching the laboratory at New York University. DNA was extracted from the packed cell samples using a standard phenol chloroform extraction (Maniatis, et al., 1982). All extracted samples were stored at -20°C. The baboon LPL intron 7 sequence (Cole et al., 1997) was used to design a novel PCR primer pair directed against the flanking sequences of the *Alu* element insertion site. The PCR oligonucleotides employed were: upstream, 5'-TCATGTCATT-AGGATAAATGCTGG-3'; downstream, 5'-CTCCTCTCCAAATATAAATAGCTC-3'. The DNA was amplified by PCR (94°C for 1 min; 54°C for 1 min, 30 sec; 65°C for 4 min; 35 cycles).

Agarose electrophoresis

PCR products were electrophoresed in 1 × tris base glacial acetic acid, EDTA (TAE) 3% agarose gels. Each gel also included one lane with 1 µg of *Hae*III-digested ϕX 174 DNA, which was used as a molecular weight marker. The two amplified fragments were easily detected after ethidium bromide staining and recorded in a Fotodyne® Incorporated FOTO/Analyst® Investigator video system.

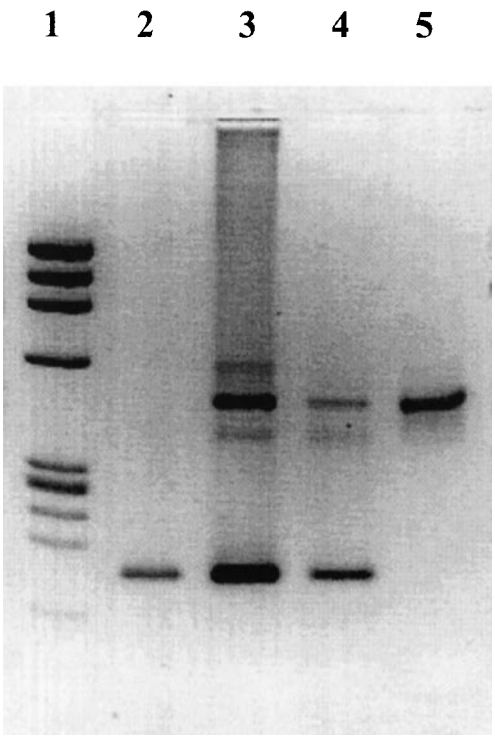

Fig. 2. Agarose gel electrophoresis separation of the LPL *Alu* insertion and lack of insertion alleles. **Lane 1,** *Hae*III-digested ϕX 174. **Lane 2,** homozygous individual for lack of insertion allele (*P. h. hamadryas*). **Lane 3,** heterozygous individual for the insertion allele (*P. h. anubis*). **Lane 4,** heterozygous individual for the insertion allele (*P. h. hamadryas*). **Lane 5,** homozygous individual for the insertion allele (*P. h. hamadryas*).

Genotyping and statistical analysis

Allelic frequencies were determined by the gene counting method (Nei, 1987). Hardy-Weinberg equilibrium probability values, locus heterozygosity, and *G*st values were generated using Biosis version 1.7 (David L. Swofford, Center for Biodiversity, Illinois Natural History Survey, Champaign, IL). The probability values for the differences between the observed and expected heterozygosity values were obtained using Microsoft™ Excell 97.

RESULTS

PCR amplification produced two distinct bands, one of 471 bp containing the insertion and the other of 160 bp, lacking the *Alu* element (Fig. 2). The novel PCR primer pair employed in the PCR reactions resulted in bands that were much easier to characterize than the bands obtained with the previously used and published primer set (Cole et al., 1997). This improvement was partly due to the smaller size of the PCR products. This decreased the duration of the electrophoretic run, and also potentially increased the amount of PCR products.

The allelic frequencies of the *Alu* insertion for each class of individuals are presented in Table 1. The insertion frequency was 0.560 and 0.780 for *P. h. anubis* and *P. h. hamadryas,* respectively. The hybrid class had an intermediate insertion frequency of 0.691. Additionally, the three classes were divided according to the collection date, which spanned 24 years, representing 2–4 generations. The insertion frequency for *P. h. hamadryas* increased over this time period from 0.769 to 0.796 (though it should be noted that the *hamadryas* groups sampled in different years were from different and widely separated regions), while in *P. h. anubis* it decreased from 0.595 to 0.469. Hardy-Weinberg equilibrium tests were performed on each of the six classes as well as on the totals for the subspecies and hybrids. All classes were in equilibrium (for *p* values, see Table 1). All hybrid classes and all *P. h. anubis* classes except the 1973 *P. h. anubis* showed higher observed than expected heterozygosity values, while all *P. h. hamadryas* and the 1973 *P. h. anubis* exhibited lower than expected heterozygosity values. Chi-square analyses for the differences between observed and expected heterozygosity are provided in Table 1. Only the 1995 hybrid group showed significance at the 5% level.

DISCUSSION

As shown in Table 1, the *Alu* repeat segregates with variable insertion frequencies across the different groups. *P. h. anubis* has a relatively low insertion frequency of 0.560, while *P. h. hamadryas* has a much higher insertion frequency of 0.780. As expected, the insertion frequency in the hybrids is intermediate to those of the parental classes.

Previously published work investigated *Mandrillus* and *Macaca* to determine whether this *Alu* insertion was present in these genera, which are closely related to

TABLE 1. Distribution of Alu insertion

Population	Polymorphic LPL *Alu* insertion locus						
	n[a]	*fAlu*	P[b]	Het_{obs}[c] ± SE[d]	Het_{exp}[e]	P[f]	Het_{obs}/Het_{exp}
1973 *anubis*	42	0.595	0.877	0.476 ± 0.043	0.482	0.938	0.988
1995 *anubis*	16	0.469	0.697	0.563 ± 0.043	0.492	0.606	1.144
Total *anubis*	58	0.560	0.963	0.500	0.493	0.909	1.014
1973 *hamadryas*	39	0.769	0.066	0.256 ± 0.001	0.355	0.196	0.721
1997 *hamadryas*	27	0.796	0.243	0.259 ± 0.001	0.325	0.467	0.797
Total *hamadryas*	66	0.780	0.036	0.258	0.343	0.143	0.752
1973 hybrid	37	0.676	0.556	0.486 ± 0.034	0.438	0.552	1.110
1995 hybrid	18	0.722	0.125	0.555 ± 0.034	0.401	0.022	1.384
Total hybrid	55	0.691	0.174	0.509	0.427	0.076	1.192
Total no. of individuals	179						
Locus Het[g]	0.429 ± 0.044						
Gst[h]	0.050						

[a] Number of individuals typed.
[b] Hardy-Weinberg equilibrium probability values.
[c] Observed heterozygosity.
[d] Observed heterozygosity standard error for the *anubis*, *hamadryas*, and hybrid populations.
[e] Expected heterozygosity.
[f] Probability values for the differences between observed and expected heterozygosity values.
[g] Observed heterozygosity for the LPL locus, averaged over all nine groups, and the standard error (±SE).
[h] *G*st value for the LPL locus for all nine groups.

baboons. The study revealed that only the baboons had the insertion (Cole et al., 1997). The analysis by Purvis (1995) estimated that baboons diverged from other Old World monkeys around 6–7 Ma, which places the date of insertion no older than this coalescence time, since if it predated the divergence of the *Papio* from the *Mandrillus* and *Macaca* lineages, the insertion would be present in these groups as well, and most likely would be monomorphic for the insertion.

In addition, this *Alu* insertion was detected in *P. h. hamadryas*, *P. h. anubis*, *P. h. cynocephalus*, and *P. h. ursinus* (Cole et al., 1997). The five subspecies of *P. hamadryas* (*P. hamadryas papio* and the four listed in the previous sentence) inhabit a large area of sub-Saharan Africa in a large geographical continuum in the shape of a "7". *P. hamadryas papio* occupies a region encompassing much of West Africa, *P. h. anubis* a band running across Africa in a west to east manner, *P. h. hamadryas* a region encompassing Egypt and Ethiopia, *P. h. cynocephalus* an area south the *anubis* range, and *P. h. ursinus* in South Africa. These subspecies are parapatric in the sense that they have limited areas of overlap within which hybridization commonly occurs. The emergence of the five known *P. hamadryas* subspecies occurred at least 200,000 years ago (Jeffrey Rogers, Southwest Foundation for Biomedical Research, personal communication). Considering that gene flow exists between all five subspecies (Jeffrey Rogers, personal communication), it is not possible to ascertain if the presence of the insertion in four of the five subspecies is due to an insertion event prior to subspecies formation or to a more recent insertional event (≤200,000 years ago) followed by gene flow and dispersion of the insertion.

Levels of heterozygosity are particularly informative. When the observed level of heterozygosity is compared to the expected, all hybrids and all *anubis* groups except for the 1973 *anubis* appear to have higher than expected heterozygosity. On the other hand, 1973 *anubis* and all *hamadryas* groups appear to have lower than expected heterozygosity (Table 1). Most of the differences between observed and expected heterozygosity in the different groups in Table 1 were not found to be statistically significant at the 5% level. This most likely is a result of the limited number of organisms available for our study.

Higher observed than expected heterozygosity is indicative of gene flow, both "normal" conspecific outbreeding as well as rarer hybridization. Conversely, lower observed than expected heterozygosity may represent inbreeding and lack of gene flow. Although heterozygosity data from a single locus are ordinarily not enough to make statements

about asymmetric gene flow (Nei, 1987), our study supports previous findings with microsatellite DNA markers (Woolley-Barker, 1998) and behavioral studies (Kummer, 1990; Phillips-Conroy et al., 1991) that indicate that levels of outbreeding are significantly higher in *anubis* than in *hamadryas* baboons. Thirty years ago, Kummer (1968) described for the first time preferential matings that could lead to the flow of genetic information from *P. h. hamadryas* to *P. h. anubis*. These observations have been substantiated by other investigators (Phillips-Conroy et al., 1991). Since baboon females have mating preference for *hamadryas* and hybrid males with *hamadryas* physical characteristics (Phillips-Conroy et al., 1991), gene flow and introgression should take place from hybrid males to pure *anubis* females, introducing *hamadryas* DNA to the *anubis* gene pool. This process would explain the apparently higher than expected number of heterozygous individuals in the hybrid groups, which reaches statistical significance in the 1995 hybrid group after several decades of observed hybridization. As would be expected, it is also the 1995 *anubis* population that exhibits greater than expected numbers of heterozygotes. In addition, it is interesting to point out that as the levels of observed heterozygosity increased from 1973 to 1995 in hybrids and *P. h. anubis*, the frequency of the LPL *Alu* insertion increased concomitantly. These findings are also consistent with differences in the social, dispersal, and mating behaviors of these two subspecies.

Anubis males live in extended multimale, multifemale groups, and migrate from their natal group at maturity. Females are philopatric, staying in their natal group with their matrilineal kin, and may mate with several males during estrus (Packer, 1977; Pusey and Packer, 1987). *Hamadryas* are highly unusual among papionins in that most males remain in their natal group (or band) to breed. Here, they maintain a small polygynous harem (a one-male unit, or OMU (Kummer, 1990)). Clusters of males and their OMUs form clans, which often forage and travel together (Sigg et al., 1982). A number of these clans make up a band, which seems analogous to the *anubis* group (Kummer, 1990; Sigg et al., 1982). A number of multiclan bands share a sleeping site and make up an impermanent troop. This flexible social order appears to be an adaptation to the *hamadryas*' desert habitat with its sparse food and water resources (Jolly, 1963; Kummer, 1990). Prepubescent females are normally recruited to an OMU within the same clan or band, often by a young "follower" male of her natal band, who is tolerated by the leader male. Later, she may pass to another male of her own clan or band, or rarely, a neighboring band. There are no obvious matrilineages at any level of the society.

These subspecies-specific social differences appear to be key factors influencing the direction and dynamics of hybridization in the zone. Differences in mating and/or social behavior may restrict gene flow between populations. These factors may be more effective in one species or subspecies than another, and may be more strongly directed against one sex than another, resulting in asymmetrical gene flow (e.g., Lamb and Avise, 1986). In the Awash National Park, the absence of mtDNA introgression (Newman and Disotell, 1997), combined with clear phenotypic evidence of hybridization, indicates that gene flow occurs in both directions through male migration. Observations of male crosspopulation migrants support this view (Kummer et al., 1970; Beyene, 1993; Nystrom, 1992; Phillips-Conroy and Jolly, 1986; Phillips-Conroy, personal communication).

P. h. hamadryas males are known to migrate into *anubis* groups and successfully maintain harems containing *P. h. anubis* females (Nystrom, 1991, 1992; Phillips-Conroy et al., 1991). *P. h. anubis* males attempt to mate with *hamadryas* females only when they are in estrus, and may have difficulty gaining access due to continual *hamadryas* male vigilance (Kummer et al., 1970; Nagel, 1973). This suggests that there may be asymmetrical introgression, with greater gene flow from *hamadryas* into *anubis* groups, rather than the reverse. The higher heterozygosity level in *P. h. anubis* presented here is consistent with these observations. However, since behavioral and genetic evidence indicate that *anubis* are strong

outbreeders, with male dispersal at maturity providing extensive gene flow (Pusey and Packer, 1987; Woolly-Barker, 1998), while strong male (and to a lesser degree female) philopatry in *hamadryas* leads to localized inbreeding and population subdivision (Woolley-Barker, 1998), it is not possible to separate the effects of "normal" outbreeding from hybridization between the subspecies.

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